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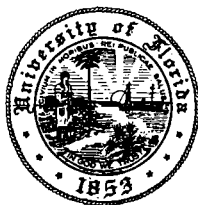
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FOSSIL TESTUDININE TURTLES OF FLORIDA
GENERA GEOCHELONE AND FLORIDEMYS

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FOSSIL TESTUDININE TURTLES OF FLORIDA GENERA *GEOCHELONE* AND *FLORIDEMYS*

WALTER AUFFENBERG¹

SYNOPSIS: Recent paleontological work in Florida has made available a large series of fossil tortoises from one relatively small area. Two distinct species of tortoises of the genus *Geochelone* are represented in the known Pleistocene localities of the area, *Geochelone crassiscutata* (Leidy) and *G. incisa* (Hay). The only valid Pliocene species of this genus is *Geochelone hayi* (Sellards). The Florida Miocene contains only *Geochelone tedwhitei* (Williams).

These four species seem to represent two main evolutionary lines. Both lines are recognized as distinct subgenera, *Hesperotestudo* and *Caudochelys*; the latter is new. *G. incisa* is the last representative of *Hesperotestudo*, a line possibly beginning with *G. amphithorax* (Cope) of the Oligocene of Colorado, and continuing through *G. osborniana* (Hay) and related forms of the late Tertiary. The new subgenus *Caudochelys* is represented in the Florida Pleistocene by *G. crassiscutata*. The subgenus can be traced from *G. ligonia* (Cope) of the Oligocene of Colorado through *G. tedwhitei* of the late Tertiary of Florida, and related species of middle and western North America.

Floridemys nanus (Hay) is known only from the Florida Pliocene. Its relationships remain obscure.

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INTRODUCTION

Fossil turtles, especially Pleistocene forms, have been so little studied that much remains to be learned of them. No single comprehensive study of tortoises, fossil or Recent, has ever been attempted. The best analysis of the generic relationships within the group is presented by Williams (1950, 1952) and Loveridge and Williams (1957). Many of the early publications tend to obscure relationships of fossil and Recent forms under a profusion of new names, often on such fragmentary individuals that identification of new material is almost impossible. This is particularly true in Florida, where six species have been described from Pleistocene deposits alone.

As outlined by Loveridge and Williams (1957) the genus *Geochelone* seems to represent a natural group. The Recent range includes the Galapagos Islands, South America, Africa, Madagascar, and certain islands of the Indian Ocean. The fossil record is fairly extensive; tortoises are well represented in the Tertiary and Pleistocene of North America and in the Tertiary of Europe, Asia, and Africa. In South America fossil tortoises date from the Miocene, and in the West Indies from the Pleistocene.

The genus includes 13 subgenera (Williams, 1950, 1952; Loveridge and Williams, 1957). Five occur in the New World (*Hadrianus*, *Hesperotestudo*, *Chelonoides*, *Caudochelys*, and *Monachelys*). The only extant New World subgenus (*Chelonoides*) is known from the Miocene to the Recent of South America, and the Pleistocene and Recent of the West Indies. *Monachelys* is a distinctive subgenus known only from the Pleistocene of the island of Mona, West Indies. So far as known, all fossil species of the genus from North America belong to the subgenera *Hadrianus*, *Caudochelys*, or *Hesperotestudo*. The first of these is considered to be the most primitive of the entire genus, and may be ancestral to the other New World groups. At present it is known only from the Eocene of North America.

Hesperotestudo, the subgenus to which *Geochelone incisa* belongs, represents a highly specialized line that differentiated early and is now extinct. The number of valid species is uncertain, but the group can be traced back into the Lower Oligocene of Colorado.

The subgenus *Caudochelys* (described herein as new) is represented in the Pleistocene, Pliocene, and Miocene of Florida, as well as in deposits of the Great Plains. It also can be traced to the Lower Oligocene of Colorado. Unlike *Hesperotestudo*, *Caudochelys* is not known from Asia. The subgenus differs from *Hesperotestudo* chiefly in that the dermal ossicles of the supracaudal area are not fused.

The following forms have been described from Florida.

Miocene testudinine remains from Florida are known at present only from the Thomas Farm, Gilchrist County. Only one species is known from this locality, *Geochelone tedwhitei* (Williams, 1953).

Only three testudinine turtles are described from Pliocene deposits of Florida. These are *Geochelone hayi*, *G. louisekressmani*, and *Floridemys nanus*. It is shown later that *G. louisekressmani* is probably a synonym of *G. hayi*.

Six testudinine turtles are described from the Pleistocene of Florida. These are *Geochelone incisa*, *G. crassiscutata*, *G. sellardsi*, *G. luciae*, *G. ocalana*, and *G. distans*. *G. incisa* remains a valid species as described. All the others are considered synonyms of *G. crassiscutata*.

Another nominal testudinine genus must be considered in discussing the Florida material.

Eupachemys obtusus Leidy (1877) is based on a single peripheral of a large turtle believed to be a testudinine from the Ashley River beds of South Carolina. These beds contain fossils of various ages, but most of the terrestrial vertebrates are Pleistocene. As the fragment lacks definitive characteristics, it cannot be assigned with certainty to any particular genus. Leidy believed it represented a large aquatic emydine turtle. Hay (1908) refers it to *Testudo* (= *Geochelone*) on the basis of size and suggests it may belong to the same species Leidy (1889) described as *Testudo crassiscutata*. This interpretation is also followed in the present study.

ACKNOWLEDGMENTS AND ABBREVIATIONS

The following abbreviations are used when referring to collections: ACM—Amherst College Museum; AMNH—American Museum of Natural History; FGS—Florida Geological Survey; MCZ—Museum of Comparative Zoology; UF—University of Florida Collections; UMMP—University of Michigan Museum of Paleontology; USNM—United States National Museum. I wish to thank the persons responsible for the collections in these institutions for the loan of specimens in their care. Special acknowledgment is due for the criticisms and suggestions made by Claude Hibbard, Ernest E. Williams, William Milstead, Clayton Ray, William J. Riemer, and Thomas Oelrich, and to the National Science Foundation for financial assistance (G-17613).

MATERIAL EXAMINED

This study is based on the recent discovery of much better material of *Geochelone* than has heretofore been available. This new material

includes many complete but isolated elements; several plastra, carapaces, and complete shells, many associated with limb elements and vertebrae. Some specimens are so well preserved that for the first time it is possible to describe the skull and the limb and circumcloacal armor. I have examined all the type material from Florida (except that of *G. louisekressmani*) as well as 18 complete shells, 18 complete plastra, and numerous isolated elements.

The University of Florida Collections contains a fine series of 12 complete or almost complete shells (some with skulls) from chronologically equivalent Pleistocene localities near Haile, Alachua County, Florida (Haile VIII A, IX, and XI). The series constitutes the largest and best sample yet assembled of any Pleistocene testudinine from a single locality in North America. Also in the University of Florida Collections are complete shells from scattered localities in Florida, and a series of plastra from a locality near Reddick, Marion County, Florida (Reddick I A).

In addition to this excellent material, many scattered elements from other localities were examined.

SPECIMENS OF *G. CRASSISCUTATA* AND *G. INCISA* EXAMINED

Type, *G. crassiscutata* USNM 983, along Peace Creek, near Arcadia, Hardee Co., Florida.

Type, *G. incisa* USNM 8821, near Ocala, Marion Co., Florida.

Arredondo II, *G. incisa* UF uncat., two epiplastra.

Eichelberger Cave B. *G. crassiscutata* UF 1457, peripheral.

Haile II B. *G. incisa* UF 3005, buckler and caudal vertebrae.

Haile VIII A. *G. incisa* UF 2986, 3029, 3132, partial shells; UF 3073, 3077, shell and limbs; UF 3141, complete skeleton; UF 3258, 3857, bucklers; UF uncat., two xiphiplastra; UF 3228, partial shell and limb elements. *G. crassiscutata* UF 3133, two scapulae; UF uncat., scapula; UF 3028, 3151, 3226, 3623, shells and limbs; UF 3139, 3623, shells; UF 3146, plastron and partial shell; UF uncat., three epiplastra; UF 3243, partial plastron; UF 3797, humerus; UF 3825, 3830, xiphiplastra; UF uncat., six xiphiplastra; UF uncat., thigh armor.

Haile IX A. *G. incisa* UF 3234, 3235, two shells with bucklers and parts of skeletons.

Haile XI A. *G. incisa* UF 3462, complete shell, buckler, and all limb elements; UF 3844, buckler.

Hillsborough River State Park. *G. crassiscutata* uncataloged, large shell in collection of Hillsborough River State Park.

Itchucknee River. *G. incisa* UF 2713, xiphiplastron. *G. crassiscutata* UF 2328, xiphiplastron; UF 1994, epiplastron.

5 mi. W Jupiter Inlet. *G. crassiscutata* UF 3006, xiphiplastron.

Kanapaha C. *G. crassiscutata* UF 9907, scapula.

Mefford Cave II. *G. crassiscutata* UF 6523, miscellaneous parts of shell.

Melbourne. *G. crassiscutata*, large complete shell in Amherst College Museum.

Prairie Creek. *G. crassiscutata* UF 1816, parts of plastron.

Reddick I. G. *incisa* UF 4748, peripherals; UF 2545, epi- and xiphi-plastron. *G. crassiscutata* UF 2477, 2532, partial carapace (?*crassiscutata*); UF 2516, 2517, 3082, 3083, plastra; UF 2397, 2420, 2480, plastra with carapace parts; UF 2460, carapace parts; UF 2851, scapula; UF 3784, femur; UF 2475, circumcloacal armor; UF 3091, xiphiplastron; UF 2598, peripherals; UF 2521, suprapygial and entoplastron.

Reddick II. G. *crassiscutata* UF 9908, small shell with crushed skull and limbs. Rock Springs. *G. crassiscutata* USNM 11311, parts of carapace and plastron of large specimen.

Zuber. *G. incisa* UF 5020, epiplastron.

Because of the fine series of specimens from the Haile VIII A locality, I decided that the best approach was to study these relatively complete specimens intensively. Fragmentary specimens, isolated finds of reasonably complete individuals, and isolated single elements could then be interpreted in the light of information gleaned from this series.

ANATOMICAL RESUMÉ OF THE HAILE SERIES

Even casual observation of the shells available from this locality leads one to the conclusion that two forms are represented. Shells of both forms occur throughout the deposit, and there is no evidence of morphological intermediacy. The degrees of plastral concavity show that males and females of both forms are present. Although one form apparently attains a much greater size than the other, all small individuals can be readily separated into two groups. These data are interpreted as being evidence of differences at the species level. The type specimens of previously described Pleistocene species of this genus from Florida, in almost every case, can be placed in one group or the other.

The earliest names for identifiable fragments belonging to these groups are *Geochelone incisa* (Hay) and *Geochelone crassiscutata* (Leidy). A comprehensive description of the specimens referred to each of these species among the Haile VIII A series is given below. The reasons for allocation of the particular names used for these two forms, and the disposition of remaining named Pleistocene forms will follow. In this series five complete or almost complete specimens are referred to *G. incisa*, while six are referred to *G. crassiscutata*.

SHELL

Specimens of this series placed in *Geochelone incisa* are much smaller than the largest placed in *G. crassiscutata*. See table 1. The largest specimen of *G. incisa* in the Haile series (UF 3141) measures 241 mm in carapacial length. The largest complete shell of *G. crassiscutata* from the same locality (UF 3623) measures 1210 mm in carapacial

TABLE 1. Shell measurements (in millimeters)

	G. incisa							G. crassiscutata						
	UF 3462	UF 3141	UF 3077	UF 3073	UF 3029	UF 2986	UF 3235	UF 3151	UF 2480	UF 2397	UF 3139	UF 3226	UF 2420	UF 3028
Carapacial length	—	241	231	228	224	216	212	327	—	—	192	180	—	168
Plastral length	264	205	214	204	206	192	196	304	259	257	180	169	164	153
Entoplastral length	52	41	42	40.5	41	39	33	72	59	55	46	38	34	39
Entoplastral width	46	36	36	36	40	40	34	71	57	55	39	39	31	32
Gular length	46	34	36	37	30	30	34	54	39	43	31	27	24	28
Humeral length	37	36	48	32	35	34	33	54	51	45	31	30	29	29
Pectoral length	11	18	12	10	7.5	12	11	19	20	14	9	7	12	13
Abdominal length	94	66	59	74	65	70	68	115	79	89	68	63	59	52
Femoral length	42	38	32	32	28	32	28	41	43	31	23	21	19	24
Anal length	16	10	9	8	12	7	12	17	22	21	9	13	19	12
Xiphiplastral notch depth	28	22	23	21	23	12.5	20	24	12	13	14	6	12	8
Xiphiplastral external height	28	23	22	21	29	19	18	24	21	21	16	14	13	12
Xiphiplastral length	33	35	35	30	35	29	32	51	43	45	33	30	33	26
Epiplastral length	51	45	50	41	49	39	40	68	60	51	29	32	32	31
Epiplastral width	47	44	43	49	40	39	39	63	57	49	38	34	31	33
Epiplastral lip thickness	36	29	28	27	31	25	21	35	31	31	17	22	19	21
Epiplastral lip length	36	33	40	31	37	39	—	45	36	36	27	23	19	21
Nuchal scute length	20	17	15	14.5	11	10	11	20	—	16	11	10	10	—
Nuchal scute width	3	8	6	7	3	9	4.5	13	—	9	9	7	9	—
Pygal length	30	29	31	22	—	27	22	44	—	—	22	21	—	19
Pygal dorsal width	40	39	46	31	—	40	28	48	—	—	26	26	—	20
Pygal ventral width	27	23	23	19	—	24	19	36	—	—	19	15	—	14
Second suprapygal length	24	19	21	19	—	31	20	27	—	—	15	14	—	24
Second suprapygal width	62	46	55	41	—	57	44	45	—	—	24	22	—	34

length, though fragments of much larger specimens have been found. Specimens referred to in *G. incisa* are more rugose than similar-sized or even larger specimens of *G. crassiscutata*. Sulcal growth patterns are much more evident in the former, the central areas of the costals are more raised, and small bosses are developed in several parts of the shell, particularly on or near the peripherals. The latter are considerably thickened, particularly the posterior members.

The plastron is also quite different in the two species. In *G. incisa* the xiphiplastral notch is much deeper (fig. 1), with the free tips more pointed. The epiplastral beak is proportionately thicker. In

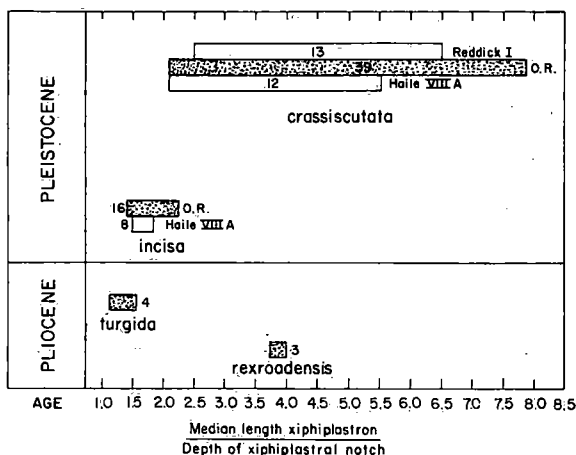


FIGURE 1. Specimens of *Geochelone* from the Pleistocene of Florida can be separated on the basis of the proportional depth of the xiphiplastral notch. The Great Plains species, *G. turgida* and *G. rexroadensis*, seem most closely related to *G. incisa* and *G. crassiscutata* respectively.

most specimens the tips of the beak are slightly divergent, and a keel may be present on each of the two elements, both dorsally and ventrally, and running out to the tips. The lateral parts of the hyo-, hypo-, and xiphi-plastral elements are thickened much more in *G. incisa* than in *G. crassiscutata* (fig. 2).

PECTORAL GIRDLE AND LIMBS

The scapulae of *G. crassiscutata* and *G. incisa* are similar. In *G. incisa* the procorocoid process is proportionally shorter than in *G. crassiscutata*. The scapular portion of the glenoid cavity is proportionally

wider in *G. incisa* than in *G. crassiscutata* (fig. 3). The included angle of the blade of the corcoid in *G. incisa* is usually smaller than in *G. crassiscutata* (measurement made with the apex of the angle located

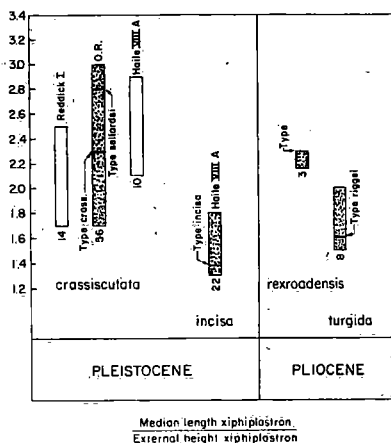


FIGURE 2. *G. incisa* and *G. crassiscutata* are readily separated on the basis of the proportional external height of the xiphoplastron.

on the shaft). Holman (1959) suggests that two humeral forms in the Florida Pleistocene indicate the presence of two species of *Geocheilone*. However, information obtained from complete specimens of all sizes of the two species indicates that the differences are usually subtle, and much ontogenetic and individual variation exists. The tuberosity in *G. incisa* seems higher than in *G. crassiscutata* in the few individuals of equal size which can be compared. The head is more rounded and set at less of an angle in *G. crassiscutata*. In early members of the Incisa group (*G. osborniana*, *G. orthopygia*), the humeral head is like that in *G. crassiscutata*.

Lack of material prevents comparison of the ulna and radius.

PELVIC GIRDLE

The lateral extent of the ventroposterior process of the ischium is greater in *G. incisa* than in *G. crassiscutata*. The extension is more acute and more twisted in the former. The anteroexternal process of the pubis tends to have a shorter articular surface in *G. incisa*, though there is age variation. Small specimens have a proportionally longer

surface. The curvature between this process and the midline is greatest in *G. incisa* (fig. 3).

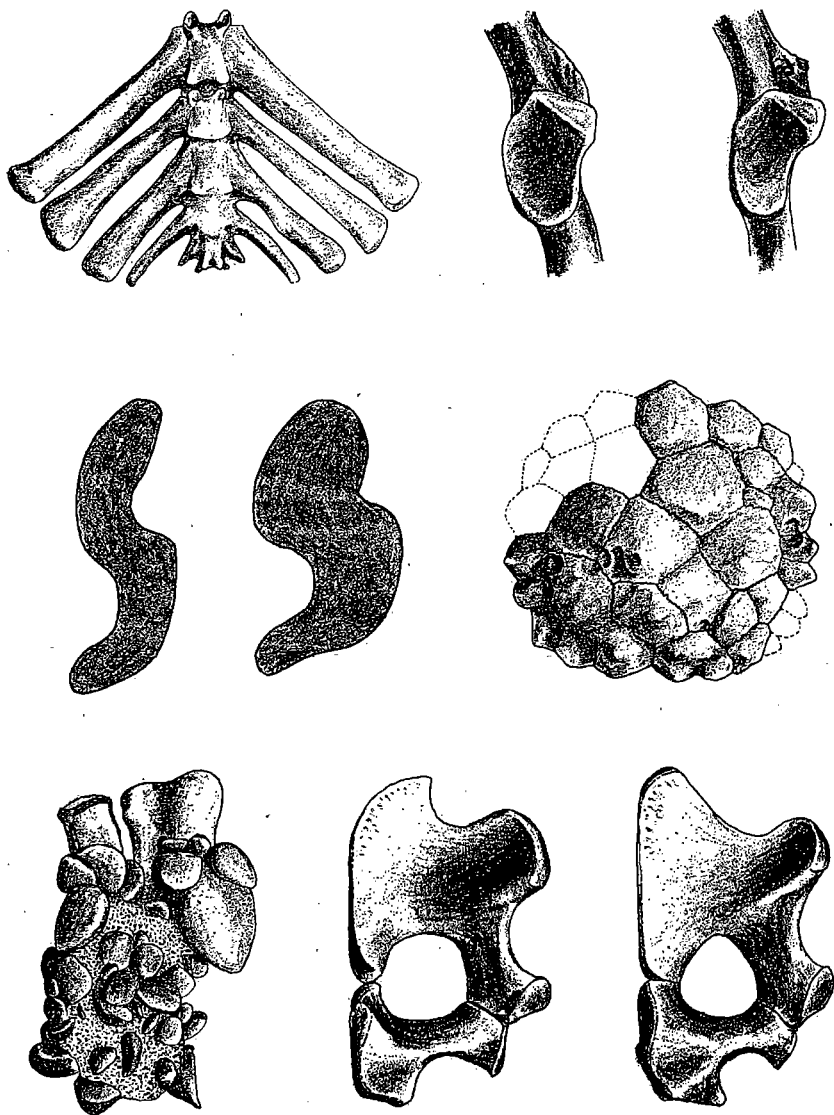


FIGURE 3.

Top left) Six fused and expanded caudal vertebrae of a specimen of *G. incisa* (UF 3077).

Top right) Proportional width of the scapular portion of the glenoid cavity in (left) *G. incisa* (UF 3077) and (right) *G. crassiscutata* (UF 3151).

The distal end of the ilium is generally thinner and less twisted in end view in *G. incisa* than in *G. crassiscutata* (fig. 3). Small specimens of the latter have ilia that are less twisted, but as far as is known, they are never as straight as in *G. incisa*.

The femur of *G. incisa* is more curved from the side, and the epicondyles are developed more than in specimens of *G. crassiscutata* of similar size. The intertrochanteric fossa is relatively much larger in *G. incisa*. The angle between the head and the external surface of the greater trochanter is greater in *G. incisa* than in *G. crassiscutata*.

In the largest available specimen of *G. incisa* (UF 3462), the fibulare is strongly co-ossified with the astragalo-calcaneum. A slightly smaller specimen of the same species (UF 3141) has this co-ossification on the left limb, but on the right the bones are only weakly united. In a similar-sized specimen (UF 3073) they are not fused. In a single specimen of *G. crassiscutata* in which the foot bones are preserved (UF 3151) these bones are not fused. Whether such fusion occurs in larger specimens of *G. crassiscutata* is unknown. Young specimens of *G. incisa* probably lack this fusion.

In UF 3462 (*G. incisa*) tarsal 3 is missing. Tarsals 4 and 5 seem to be fused. Such fusion is not present in the best hindfoot of *G. crassiscutata* examined (UF 3151). Metatarsal 3 and phalange III are fused in UF 3462.

VERTEBRAE

In *G. incisa* the terminal portion of the tail is expanded to support the heavy, co-ossified supracaudal ossicles (fig. 3). The last 5 vertebrae of *G. osborniana* have lengthened lateral processes. In *G. orthopygia* at least 6 vertebrae show these elongated processes. The last 8 vertebrae are so modified in the specimens of *G. incisa* examined. Thus, the available material of this phyletic line suggests an increase from the Miocene to Pleistocene in the number of vertebrae supporting the supracaudal buckler.

The inference by Hay (1908:426) that the lengthened transverse processes of *G. osborniana* differ basically from the "distinct, true caudal ribs" of *Gopherus polyphemus* is apparently in error. In UF 3462, an excellent specimen of *G. incisa*, most of the processes are

Middle left) Shape of the distal end of the ilium in (left) *G. incisa* (UF 3077) and (right) *G. crassiscutata* (UF 3151).

Middle right) The supracaudal buckler of *G. incisa* (UF 3077).

Lower left) The forelimb armor of *G. incisa* (UF 3141).

Lower right) Pelvic girdle of (left) *G. crassiscutata* (UF 3151) and (right) *G. incisa* (UF 3141).

firmly ankylosed to the vertebrae. However, several of the vertebrae clearly show a thickened seam at the juncture of the base of the process and the vertebral body. Furthermore, a few of the vertebrae anterior to the buckler lack the processes, whereas adjacent members possesses them. Where they are missing the articular surface of the caudal rib is clearly evident. In a small specimen of *G. incisa* (UF 3141) all the vertebrae anterior to the buckler lack the ribs but have the articular surface. In the vertebrae supporting the buckler the ribs are all firmly fused to the centra. The ribs are not fused to the centra in specimens of *G. crassiscutata* of the same size. However, in large specimens of this species these ribs are all firmly fused to the vertebrae. Thus the character seems to be associated with size, at least in the more anterior vertebrae.

Complete cervical series of both *G. incisa* and *G. crassiscutata* are available. Most individual members of the series show no differences between the two species, but the second vertebra does show a few differential characters. In *G. incisa* the prezygapophysial articular surfaces are almost horizontal when viewed from the front. In *G. crassiscutata* the surfaces are at an angle of about 45 degrees. In *G. incisa* the anterior articular surfaces of this element are sometimes biconcave (2 out of 4 complete series associated with complete shells). In *G. crassiscutata* the surfaces are biconvex in all 4 specimens examined. Many more vertebral series associated with shells are needed

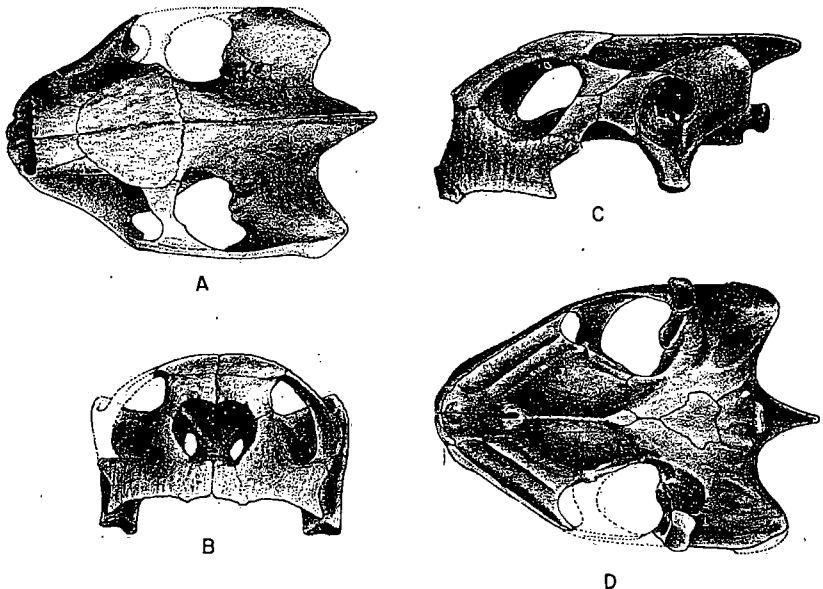


FIGURE 4. The skull of *G. incisa* (UF 3141)

to validate this suspected proportional difference in shape of the articular surfaces.

SKULL

A complete skull of *G. incisa*, associated with the rest of the skeleton and shell (UF 3141) from Haile VIII A, is rather long and narrow (fig. 4, and table 2), but less so than that in *G. osborniana*. The sides are almost parallel from the squamosal processes to the posterior border of the orbits. Near the middle of the orbits the maxillaries converge to the snout and are slightly concave from above. From the side the dorsal surface is slightly concave behind the orbits, and strongly convex above and in front of them. The cutting edge of the maxilla is concave and finely serrated. There is a low, wide notch with slightly larger serrations on either side anteriorly. The squamosal processes are slightly compressed laterally, less so internally.

TABLE 2. Measurements of the skull of *G. incisa* (UF 3141)

Snout to end of supraoccipital process	51 mm
Snout to occipital condyle	42
Width at base of quadrates	35
Width at posterior end of maxillae	33
Width of interorbital space	14
Width of nasal opening	12
Anteroposterior diameter of orbit	14
Maxillary edge to highest part of frontal	18
Median length of prefrontals	9
Median length of frontals	11
Width of jugal arch	7

The upper outer border rises above the upper surface of the paroccipital.

The height of the skull from the cutting edge of the maxilla to the upper surface of the frontals is contained in the length from the snout to the condyle 2.3 times. The anteroposterior extent of the otic region is 12 mm, and is contained in the length of the skull to the condyles 3.5 times.

The palatal region is highly vaulted, the median fossa having a width of 13 mm. The narrowest part of the pterygoids is 11 mm. The alveolar surface of the maxilla is provided with 2 longitudinal ridges and 2 grooves. The outer, larger ridge is separated from the cutting edge by the wider groove. The ridge is sharp, slightly serrated, and runs forward and inward to the premaxillary, is then directed anteriorly to the cutting edge of the same element. The inner ridge is higher than that in *G. osborniana*. It is broader posteriorly

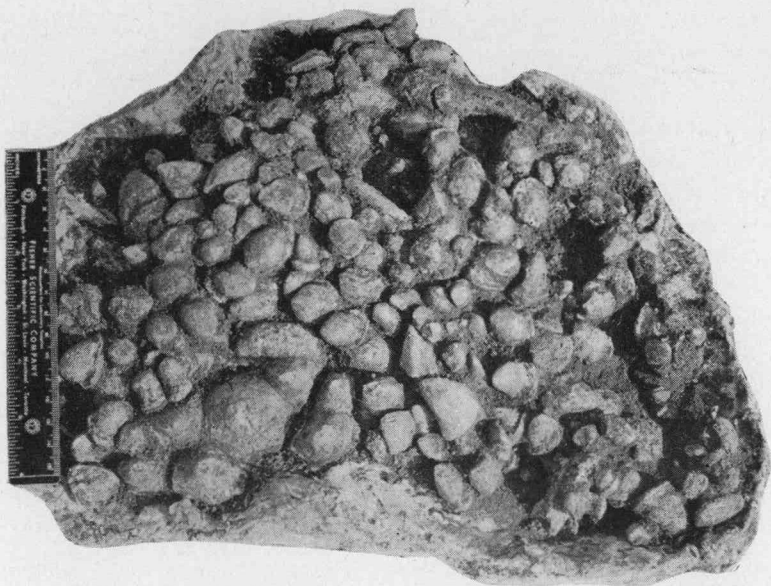


FIGURE 5. The circumcloacal armor of *G. crassiscutata* (UF 2475).

than anteriorly and runs along the inner edge of the maxillary. There is no median premaxillary ridge.

The skull of *G. incisa* is more like that of *G. osborniana* than that of *G. gilberti*, but the jugal arch is wider still than in the former. The otic region, like that in *G. osborniana*, is less elongated than in *G. gilberti*. The skull of *G. impensa* differs from *G. incisa* in the structure of the maxillary ridges, in having a narrower jugal arch, a narrower palatal fossa, wider prefrontals, and longer squamosal processes. The skull of *G. orthopygia* is like that of *G. osborniana*, and thus similar to that of *G. incisa*. In *G. orthopygia* the skull is wider than in *G. incisa*; the prefrontals are wider, and the frontals proportionally shorter. The cutting surface of the mandible is longer in *G. incisa* than in *G. orthopygia*.

A small specimen of *G. crassiscutata* in the University of Florida Collections from Reddick II (UF 9908) includes a smashed skull. Little can be determined from this specimen except that the frontal is proportionally longer than in *G. incisa*.

LIMB ARMOR

UF 3151, a half-grown *G. crassiscutata* shows some of the armor of both the front and hind limbs. The bottom of the hind foot is covered with fairly large, flat, bony plates. Those at the posterior periphery of the foot are much larger, and more spurlike than those over the rest

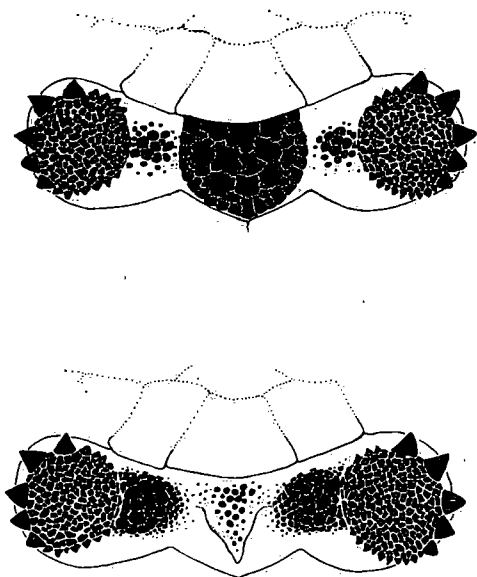


FIGURE 6. A diagrammatic illustration of the posterior limb and caudal armor shown in black in (top) *G. incisa* and (bottom) *G. crassiscutata*.

of the foot. The armor of the front limbs below the humerus is unknown in *G. crassiscutata*. However, a number of large, lanceolate, flattened scutes found with several large specimens suggests that a part of the forelimb was armored.

The thigh armor of *G. crassiscutata* is now well known. Two groups of ossicles from this region, associated with shells, are available. Both specimens are large. In each, several ossicles are fused together to form a plate on the posterior surface of the thigh. The plate is composed of approximately 12 large, highly peaked ossicles (figs. 5, 6). Around this plate the ossicles are usually smaller, though a few large spurs occur between the plate and the base of the tail.

The heel armor of *G. incisa* is unknown. The armor of the forelimb shows in UF 3141 (fig. 3) and seems to be composed of proportionally larger ossicles than in *G. orthopygia*. In fact, the ossicles on the outer edge of the limb are proportionally larger than in most extant testudinines except for a few Old World forms. The largest ossicle is contained in the length of the ulna 2.5 times.

As far as known the ossicles on the posterior surface of the thigh of *G. incisa* are not fused as they are in *G. crassiscutata*. Instead, the area seems to be covered with large, loose, conelike ossicles. As in large specimens of *G. crassiscutata*, spurs are present between this area and the base of the tail.

CAUDAL BUCKLER

One of the most diagnostic features of *G. incisa* is a fused series of dermal scutes immediately above the tail (fig. 3). The entire series comprises a subcircular patch composed of from 30 to 40 scutes. All the elements are quite firmly ankylosed in larger specimens. The scutes are pentagonal, hexagonal, or octagonal. Although there is no definite alignment, the central scutes are usually largest. Each scute near the center usually has a small spur, frequently off center. The scutes close to the edge are more conelike.

On the basis of several complete specimens in which this buckler was found in place, in life it was obviously located near the median posterior edge of the carapace. The pygal and the adjacent carapacial bones possess a transverse depression on their inner surfaces. It is presumed that the plate was hinged to the underside of the carapace along its upper edge (fig. 7).

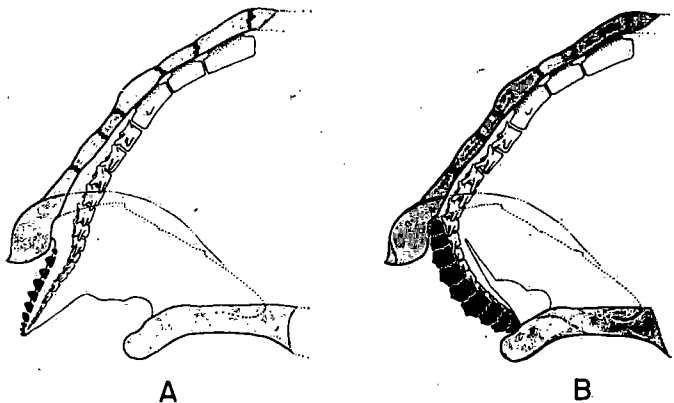


FIGURE 7. Cross-sectional views of the posterior parts of the shells of (A) *G. crassiscutata* and (B) *G. incisa* showing the diagnostic features of the caudal area.

The caudal vertebrae are closely appressed to the underside of the buckler, where the compressed and elongate transverse processes sometimes fit into shallow grooves.

A supracaudal buckler of fused scutes, with similarly modified vertebrae has been described in *G. orthopygia* and *G. osborniana* (Hay, 1908), and in *G. turgida* (Oelrich, 1957), as well as in some less well known forms. In all these species the unit is composed of fewer and more simple elements.

The tail of *G. incisa* was obviously short and probably did not show externally in life (fig. 8). The last few caudal vertebrae are much

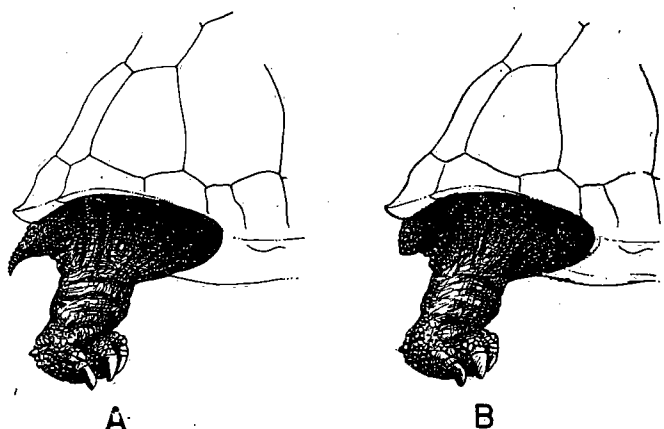


FIGURE 8. Presumed appearance, in life, of the tail of (A) *G. crassiscutata* and (B) *G. incisa*.

compressed caudocranially and do not extend beyond the posterior or ventral edge of the buckler.

Evidently two groups of tortoises of the genus *Geochelone* were present in Florida during the Pleistocene. Each group is represented by a single species, *G. incisa* and *G. crassiscutata*. These groups seem to correspond to the two lines recognized in western North America—*G. orthopygia*—*G. osborniana* and *G. ligonia*—*G. rexroadensis*. These two groups are so distinct that it seems best to recognize them as two separate subgenera. *G. osborniana* (Hay) (figs. 27, 28) is the type species of the subgenus *Hesperotestudo*, including *G. orthopygia* (fig. 29), *G. turgida* (fig. 9), *G. riggsi* (fig. 31), *G. incisa* (figs. 22, 23, 24), and all of their relatives. *G. uintensis*, *G. tedwhitei* (fig. 21), *G. rexroadensis*, *G. crassiscutata* (figs. 10, 11, 12, 13), and all of their relatives seem to form a natural group here designated as a new subgenus.

SYSTEMATICS

GENUS GEOCHELONE

Caudochelys, new subgenus

TYPE SPECIES. *Geochelone crassiscutata* (Leidy)

DEFINITION. A Nearctic subdivision of the genus *Geochelone* with a narrow nuchal scute, entoplastron about as wide as long, pectoral scutes reduced along the midline, and limbs and tail heavily armored with dermal ossicles. Ossicles above the tail are never fused to form a supracaudal buckler, and the vertebræ are normal, not

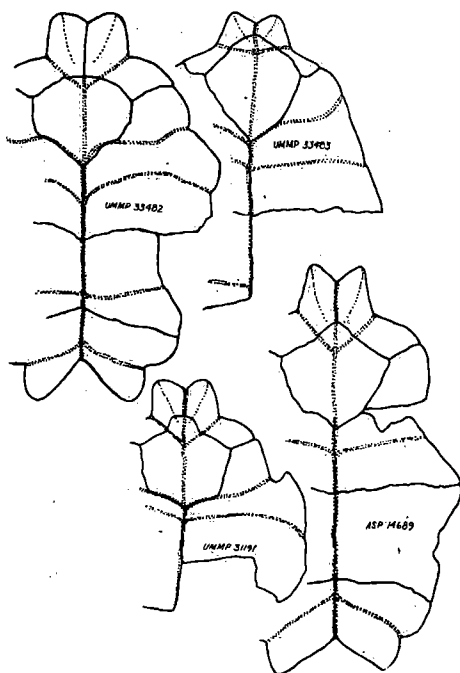


FIGURE 9. A series of plastra of *G. turgida*, showing the projected and keeled epiplastral beak also found in *G. incisa*.

compressed or fused, without greatly elongated transverse processes. Eocene to Pleistocene of North America.

Geochelone (Caudochelys) crassiscutata

Figures 10, 11, 12, 13

Testudo crassiscutata Leidy, 1889.

Testudo sellardsi Hay, 1916. Loomis, 1927; Williams, 1950.

Testudo luciae Hay, 1916. Loomis, 1927.

Testudo ocalana Hay, 1916.

Testudo distans Hay, 1916.

Gopherus ocalana (Hay) Williams, 1950.

Geochelone sellardsi (Hay) Ray, 1957.

Geochelone luciae (Hay) Ray, 1957.

Geochelone ocalana (Hay) Ray, 1957.

TYPE. USNM 983, the greater portion of the right epiplastron, a part of the right hyoplastron, parts of the posterior lobe of the plastron, the left femur and the left tibia (fig. 10).

TYPE LOCALITY AND HORIZON. Peace Creek, near Arcadia, Hardee County, Florida; Pleistocene, Recent, or both, but probably only the former.

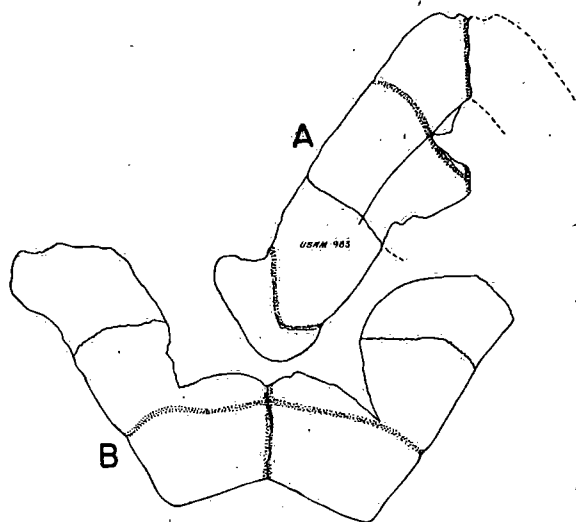


FIGURE 10. Type of *Geochelone crassiscutata* (USNM 983), (A) right epiplastron, (B) xiphiplastron.

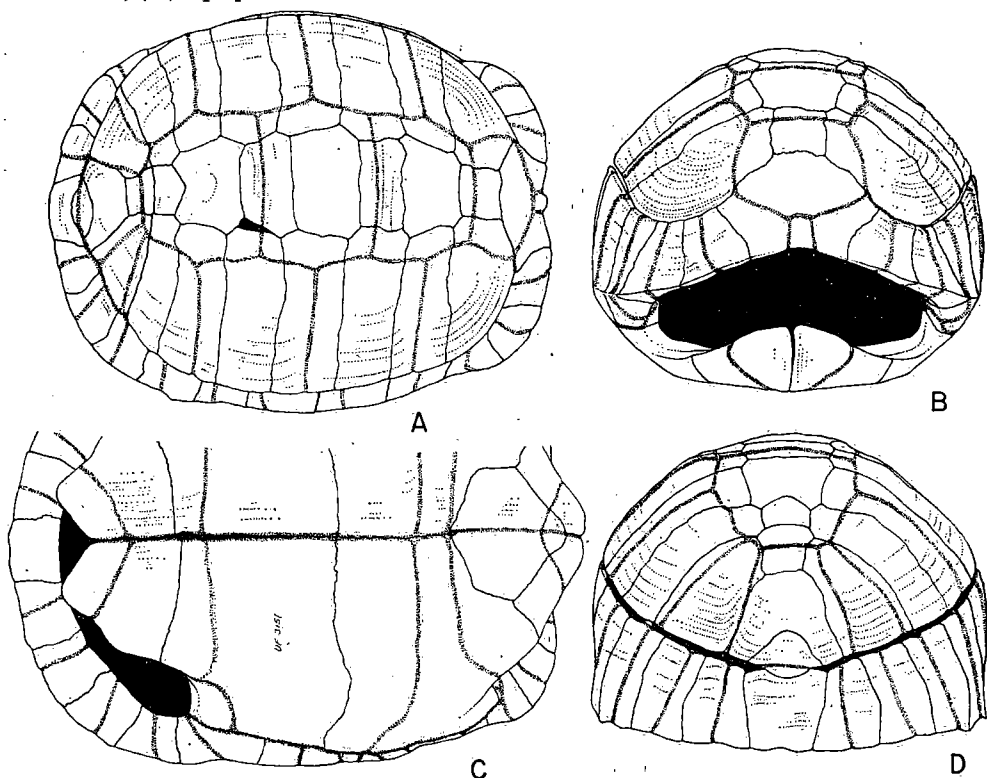


FIGURE 11. Subadult *G. crassiscutata* (UF 3151) from Haile VIII A, Alachua County, Florida.

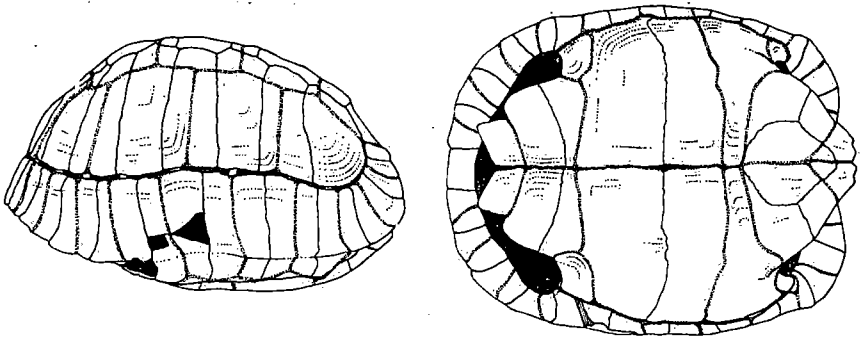


FIGURE 12. Juvenile *G. crassiscutata* (UF 3139) from Haile VIII A, Alachua County, Florida.

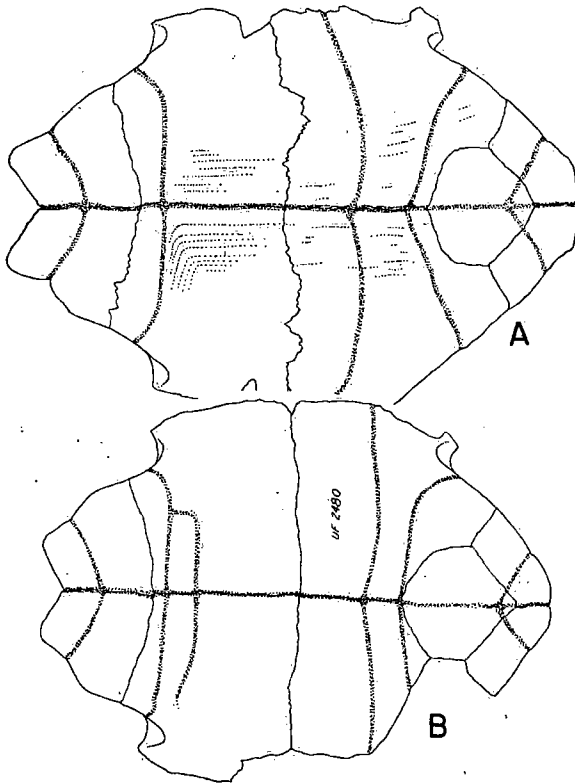


FIGURE 13. Plastra of subadult specimens of *G. crassiscutata* from Reddick I A, Marion County, Florida. (A) UF 2517, (B) UF 2480.

DIAGNOSIS. A species of giant Pleistocene testudinine, differing from *G. incisa* in being larger, having a thinner, less rugose shell, a shallower xiphiplastral notch, a less well developed and simpler epiplastral beak, a longer tail, and, in large specimens, a small fused patch of dermal ossicles on the posterior surface of the thigh. It also differs in lacking a caudal buckler.

The major differences between the two species of Florida Pleistocene tortoises are:

<i>G. incisa</i>	<i>G. crassiscutata</i>
1) Carapacial length to 231 mm	Carapacial length to at least 1150 mm
2) Supracaudal ossicles fused into a rounded caudal buckler (figs. 3, 6)	Supracaudal ossicles not fused into a caudal buckler (figs. 5, 6)
3) Caudal vertebrae fused, compressed anteroposteriorly, transverse processes attenuate (fig. 3)	Caudal vertebrae not fused, not noticeably compressed, transverse processes not as attenuate
4) Shell, and particularly the peripherals, thicker proportionally, rugose (particularly in males)	Shell thinner proportionally, smoother
5) Xiphiplastral notch deep, included angle less obtuse (fig. 1)	Xiphiplastral notch less deep, included angle more obtuse (fig. 1)
6) Epiplastral beak thicker, frequently strongly keeled	Epiplastral beak smaller, thinner, rarely keeled, and then only slightly
7) Xiphiplastron proportionally higher at outer edge of hypohyoplastral suture (fig. 2)	Xiphiplastron proportionally lower at outer edge of hypohyoplastral suture (fig. 2)
8) Width of first suprapygal greater (fig. 14)	Width of first suprapygal less (fig. 14)
9) Entoplastron narrower (fig. 15)	Entoplastron wider (fig. 15)

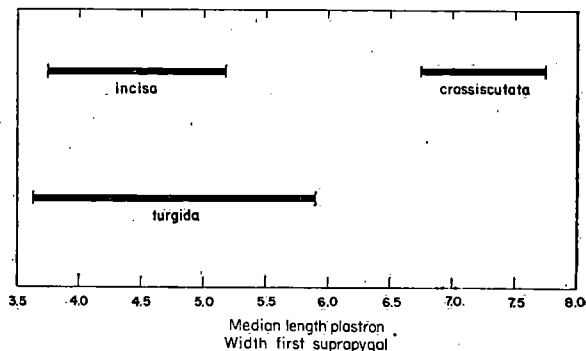


FIGURE 14. Proportional width of the first suprapygal in *G. incisa*, *G. crassiscutata*, and *G. turgida*.

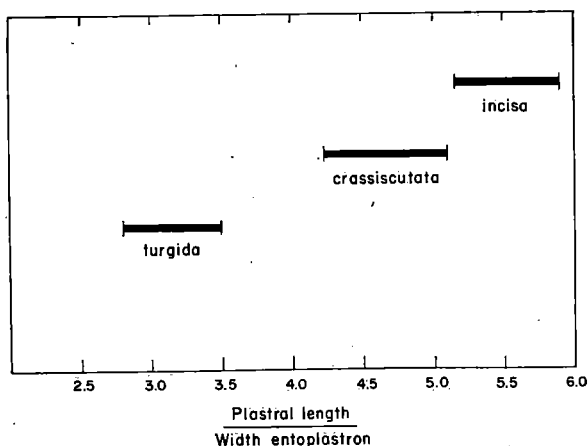


FIGURE 15. Proportional width of the entoplastron in *G. incisa*, *G. crassiscutata*, and *G. turgida*.

Both species exhibit considerable variation in many of these characteristics, usually associated with sex or size. However, some evidence in *G. crassiscutata* (in which small series are available from several localities) suggests that minor chronological or geographical differences occur in certain shell ratios (fig. 16). The two available specimens of *G. incisa* from Haile X, Alachua County, have caudal bucklers with ossicles considerably more flattened than in any specimen from Haile VIII A, Alachua County. If valid, such differences are probably indicative of chronological rather than geographical differentia-

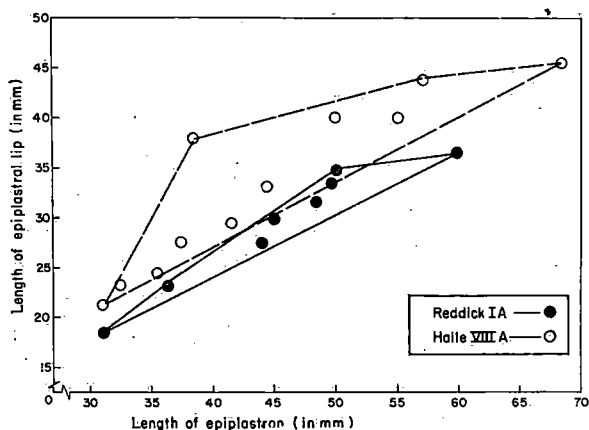


FIGURE 16. An example of minor differences in shell ratios in two populations of *G. crassiscutata*.

tion, as the localities are close to one another. Until larger series are available from additional localities such presumably minor differences cannot be critically evaluated.

Geochelone crassiscutata (Leidy, 1889) is described on the basis of fragments of three individuals collected from the shoals of Peace Creek. The original collection of specimens made by J. Francis LeBaron was numbered 983 to 986 in the United States National Museum. As Hay (1908) restricted the type material to that figured by Leidy, the type number should be USNM 983 (the number of the figured xiphiplastron, etc.), rather than USNM 985, as stated by Hay. Most of the nontype material of the same lot is catalogued as USNM 6730.

The type material includes a large part of the right epiplastron (fig. 10), a part of the right hypoplastron, parts of the posterior lobe of the plastron, the left femur, and the left tibia. These remains suggest the complete turtle probably had a carapacial measurement of approximately 1520 mm. Hay referred to the same species a number of other fragments of large testudinine turtles in the United States National Museum and the American Museum of Natural History. The preserved elements, particularly the xiphiplastron, suggest that this species represents the second major phyletic line of *Geochelone* in the Pleistocene of Florida, being closest to the Miocene *G. tedwhitei* (Williams).

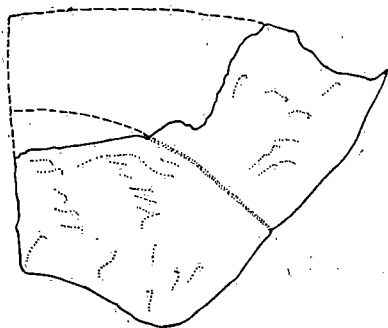


FIGURE 17. Type of *Geochelone sellardsi* (USNM 8817), a left xiphiplastron.

Geochelone sellardsi (Hay, 1916), is based on part of a xiphiplastron and parts of a carapace of a large testudinine turtle (fig. 17) collected at Vero, Indian River County, Florida (USNM 8817, formerly FGS V-1831). The diagnosis indicates that *G. sellardsi* is similar to *G.*

crassiscutata (Leidy), but differs from it (Hay, 1908) in having the outer face of the anterior part of the thickened xiphiplastral border flat or concave instead of convex. The thickness of the anterior end of the border is contained in the distance to the bottom of the xiphiplastral notch 3.6 times, instead of 3 times as in *G. crassiscutata*. Other characters mentioned by Hay as important in separating the two species are the extent of horn covering the upper surface of the xiphiplastral lobes, and the sculpturing of the lower surface of the lobes. Hay thought that the degree of sculpturing might vary between individuals. An almost complete specimen presumably representing this species was described by Loomis (1927).

The characters chosen as diagnostic of the species are now all known to be variable within a sample of one species from one locality. The name *G. sellardsi* is here referred to the synonymy of *Geochelone crassiscutata* Leidy.

Geochelone luciae (Hay, 1916) has as the type a part of the right hypoplastral element (USNM 8818, formerly FGS V-1807) of a large tortoise from Vero, Indian River County, Florida. Hay states that this species possibly attained the size of *G. crassiscutata*. He says it differs from the latter in having a thinner wall along the border of the base of the posterior lobe. However, on the type the articular surface between the hypoplastron and the xiphiplastron is broken away. Therefore, Hay's comparison of the shape of this area in *G. luciae* and *G. sellardsi* is not warranted. Furthermore, the element is one

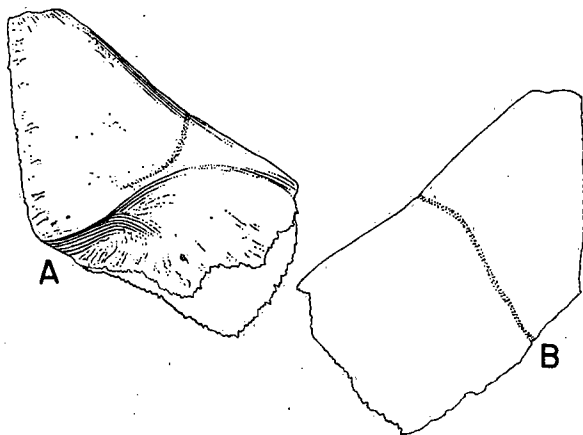


FIGURE 18. Type of *Geochelone ocalana* (USNM 8822), a right epiplastron. (A) dorsal, (B) ventral.

which shows considerable variation in thickness. Evidence shows that this variation is both individual and ontogenetic within a single species from a single locality. As no feature clearly separates *G. luciae* from *G. crassiscutata*, the name is here placed in the synonymy of the latter.

Geochelone ocalana (Hay, 1916) is the right half of an epiplastron (fig. 18) collected from a fissure in a quarry of the Florida Lime Company, Ocala, Marion County, Florida. The type is USNM 8822 (formerly FGS V-4299). According to Hay, the available material places this species closest to *G. crassiscutata* but differs from it in having a thicker epiplastral beak. The thickness of this element is extremely variable and almost useless in identification of *Geochelone* remains from Florida. A hypoplastral and first pleural from the same locality were provisionally placed in this species by Hay. Williams (1950) incorrectly placed the species in the genus *Gopherus*, but indicated that the material was so fragmentary that positive identification was impossible. The present study indicates that *G. ocalana* is best placed in the synonymy of *G. crassiscutata*.

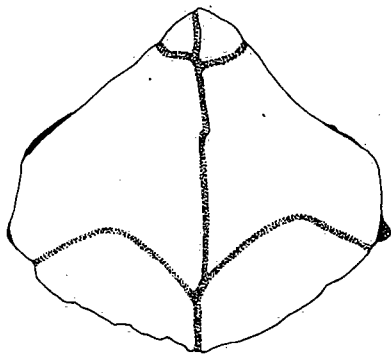


FIGURE 19. Type of *Geochelone distans* (USNM 8819), an entoplastron.

Geochelone distans (Hay, 1916). A complete entoplastron (USNM 8819, formerly FGS V-4289) is the type (fig. 19). It was collected at pit 5 of the Florida Lime Company at Ocala, Marion County, Florida. The distinguishing feature of the element is that the pectoral scutes extend anteriorly onto the entoplastron, whereas in nearly all other species these scutes have their anterior border just behind this element. The xiphiplastron is clearly from a large specimen, presumably possessing a thinner plastron than that in the type of *G. crassiscutata*. Hay was unable to compare the element with that of any other Pleis-

tocene species from Florida, except *G. ocalana*, from which it differs considerably.

The species *G. distans* is here tentatively placed in the synonymy of *G. crassiscutata* on the basis that the presumed diagnostic character occurs as a variant in several species of tortoises.

Geochelone (? *Caudochelys*) *hayi*

Testudo hayi Sellards, 1916.

Testudo louisekressmani Wark, 1929.

Gopherus hayi (Sellards) Williams, 1950. Ray, 1957.

TYPE. USNM 8815 (formerly FGS V-5001) a large portion of the posterior parts of both the carapace and plastron.

TYPE LOCALITY AND HORIZON. Amalgamated Phosphate Company pit, Brewster County, Florida; Pliocene, Bone Valley Gravel formation.

DIAGNOSIS. A large species of Pliocene testudinine turtle differing from the dwarf *Floridemyx nanus* in being much larger, and in having the gular sulcus at an angle with the midline of the plastron, rather than perpendicular to it. The xiphiplastral notch is deeper and more acute than in *G. crassiscutata*. The exterior wall of the hypoplastron of *G. hayi* is vertical, while in *G. crassiscutata* it slopes inward. The carapace of the type of *G. hayi*, though larger than that of *G. crassiscutata*, is much thinner.

Geochelone hayi represents a fairly large testudinine, estimated to have been about 1500 mm in length. The second neural is octagonal,

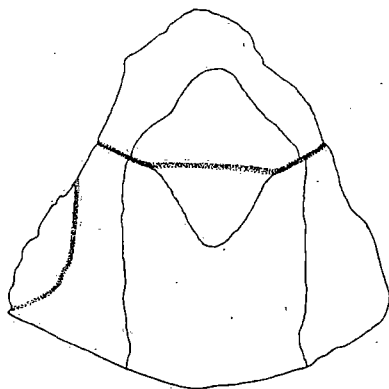


FIGURE 20. Rear portion of the carapace of the type of *Geochelone hayi* (USNM 8815) showing the correct shape of the second suprapygal.

and neurals 4 to 8 are hexagonal. The proximal end of the second pleural is slightly reduced in width and is in contact with the second neural only, while the third pleural touches neurals 2, 3, and 4. The first suprapygal is large and rests on the eleventh marginal and the pygal. The second suprapygal is considerably reduced (Sellards's [1916] figure of the type showing the posterior portion of the carapace is in error, as the second suprapygal is wider than originally illustrated [fig. 20]).

The species *G. hayi* was recently placed in the genus *Gopherus* (Williams, 1952). This interpretation is probably incorrect and *G. hayi* is here referred to the genus *Geochelone*, and tentatively to the subgenus *Caudochelys*.

Geochelone louisekressmani (Wark, 1929). This species is described on the basis of a disarticulated partial shell, including parts of the right and left halves of the epiplastron, fragments of the hypoplastron, a humerus, a pygal, several fragments of the xiphiplastron, marginals, pleurals, and vertebral scutes. All this material was collected from pit 5 of the Amalgamated Phosphate Mining Company near Brewster, Florida. Stratigraphic data are lacking, though the specimen is thought to have come from the Bone Valley Gravel formation.

Many opinions on the age and manner of deposition of this formation are published. This apparently is because of the complexity of the lithologic units. Most workers now agree that both Miocene and Pliocene vertebrates are represented in its fauna; almost all the marine forms are considered Miocene, and the terrestrial species Pliocene. Of particular importance is the fact that the same mine has also produced many remains of *Mastodon* and *Chlamytherium* (Wark, 1929), both Pleistocene genera. Local deposits of Pleistocene age apparently occur throughout this entire region; normally as shallow lenses near the top of the section and probably representing stream or pond deposits. *G. louisekressmani* conceivably could have originated from these superficial beds. It is here placed in the Pliocene, but with reservations.

The type is a poor reconstruction of a poor specimen. Wark states that the carapace is represented by the "right forepart." Unfortunately the type could not be located, but examination of the published figure suggests that it is the rear part, embracing parts of both the right and left sides. The reconstructed sulci in Wark's figure are completely in error.

The type was collected at the same mine and at the same time as

the material described by Sellards as *Testudo hayi*. Sellards refers several other fragments collected from this mine to *T. hayi*. Wark makes no reference to the type or referred material of *T. hayi*. The original number of the type of *G. louisekressmani* and also that of *T. hayi* was FGS V-5001. Hence Wark's material was either part of the type material of *T. hayi*, or at least material referred to *T. hayi* by Sellards. Unfortunately, Sellards does not describe this additional material adequately enough to be positive.

The only diagnostic characters mentioned by Wark are great size, and lack of symmetry of the peripherals, pleurals, and neurals. The type material of *G. hayi* does not represent a small testudinine, though one considerably smaller than the type of *G. louisekressmani*. Because nothing is known of the maximum size attained by *G. hayi*, the character is worthless. The lack of symmetry in various elements of *G. louisekressmani* can be explained by Wark's misinterpretation of the part of the shell represented in the type material. In proper position these elements not only seem quite symmetrical, as far as can be determined, but are similar to the same elements in the type of *G. hayi*. Therefore, the name *Testudo louisekressmani* Wark is here referred to the synonymy of *Geochelone hayi* (Sellards).

The University of Florida Collections has additional material referred to this species from several localities. This includes several isolated elements and fragments of the shell of an individual collected at Haile VI A, near Haile, Alachua County, Florida; a few peripherals from the Camp 12 Mine, near Holder, Citrus County, Florida; and a few fragments from the McGehee property, a few miles north of Newberry, Alachua County, Florida. None of these fragments gives any additional information on variability in the specific characters of *G. hayi*.

Geochelone (Caudochelys) tedwhitei

Figure 21

Testudo tedwhitei Williams, 1953.

Geochelone tedwhitei (Williams) Ray, 1957.

TYPE. MCZ 2020, a complete plastron.

TYPE LOCALITY AND HORIZON. Thomas Farm, Gilchrist County, Florida; Arikareean, Lower Miocene; Hawthorne formation.

DIAGNOSIS. A medium-sized Miocene species of testudinine with gulars more triangular and the ends smaller than in *G. crassiscutata*. It differs from *G. hayi* in being smaller and in the shape of the suprapygals.

REMARKS. Most of the following data comes from Williams (1953). As far as known, *G. tedwhitei* does not exceed 400 mm in plastral length. The length of the median sulcus of the abdominals is 6 to 7

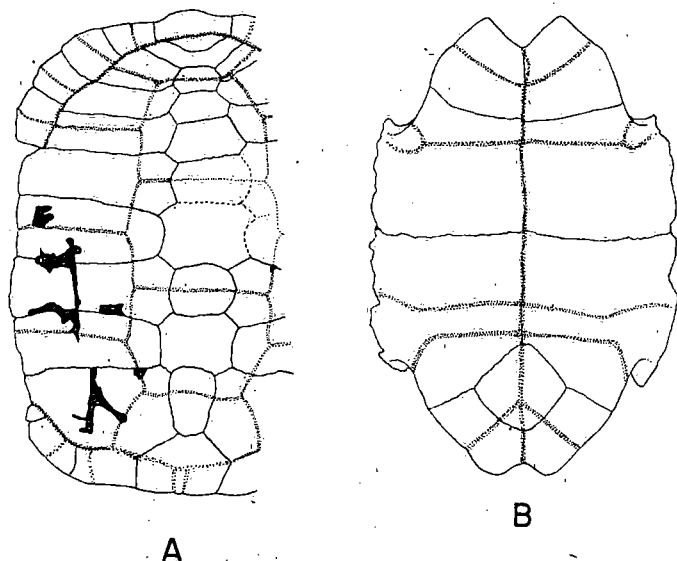


FIGURE 21. *Geochelone tedwhitei*. (A) Carapace. (B) Type plastron (MCZ 2020). Both from Lower Miocene, Thomas Farm, Gilchrist County, Florida.

times that of the pectoral scutes. The gulars are more nearly triangular and the anals smaller than *G. crassiscutata*. The well developed nuchal scute reaches the anterior margin, and the costovertebral sulci are not deeply incised. The free margins are less reverted than in *G. crassiscutata*. Several plastra and an almost complete carapace are available. *G. tedwhitei* is apparently most closely related to *G. farri* and *G. ducatelli*.

Subgenus *Hesperotestudo* Williams

TYPE SPECIES: *Geochelone osborniana* (Hay).

DEFINITION. A Nearctic subdivision of the genus *Geochelone* with a narrow nuchal scute, an entoplastron about as wide as long, reduced pectoral scutes, and limbs and tail heavily armored with dermal ossicles. Those above the tail are fused to form a supracaudal buckler; the tail vertebrae are compressed, sometimes fused. The transverse processes of the caudal vertebrae are greatly elongated. (?)Eocene to Pleistocene of North America, and "Tertiary" of Asia.

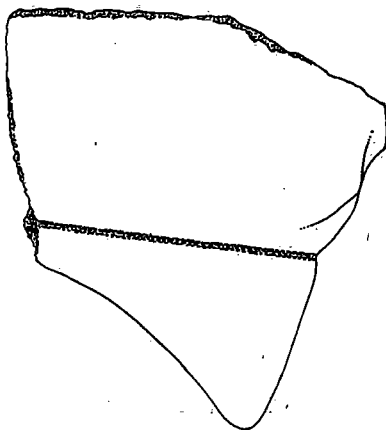
Geochelone (Hesperotestudo) incisa

Figures 22, 23, 24

Testudo incisa Hay, 1916.*Gopherus incisa* (Hay) Williams, 1950.*Geochelone incisa* (Hay) Ray, 1957.

TYPE. USNM 8821, a complete left xiphiplastron (fig. 22).

TYPE LOCALITY AND HORIZON. Pit 5, Florida Lime Company, Marion County, Florida; Pleistocene.

FIGURE 22. Type of *Geochelone incisa* (USNM 8821), a left xiphiplastron.

DIAGNOSIS. A species of Pleistocene testudinine differing from *G. crassiscutata* in being smaller, more rugose, with a thicker shell, sometimes with bosses on some of the peripherals and on the bridge; the epiplastral beak is proportionately thicker, frequently with a keel above and below, and with acute tips that are more divergent than in *G. crassiscutata*; the xiphiplastral notch is deeper, the enclosed angle being less than in *G. crassiscutata*; the entoplastron is proportionally longer in *G. incisa*; the interanal sulcus is shorter; the buttress at the outer anterior edge of the xiphiplastron is proportionally much higher. In life the tail may not have been noticeable externally; the last few caudal vertebrae are shortened and fused; the transverse processes are larger than in *G. crassiscutata*. Ossicles of the posterior surface of the thigh are not fused into a single unit, and a number of ossicles above the tail are fused into a plate that is absent in *G. crassiscutata*.

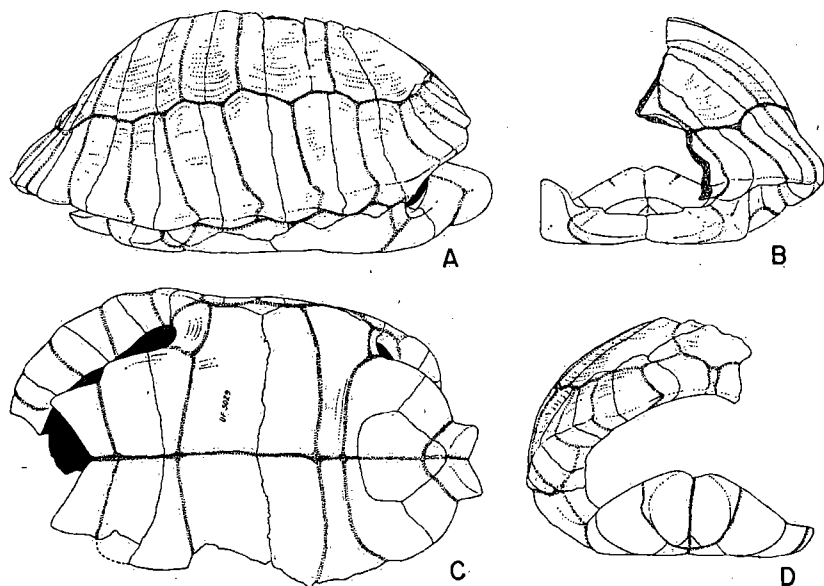


FIGURE 23. Shell of adult *G. incisa* (UF 3029) from Haile VIII A, Alachua County, Florida. (A) lateral, (B) posterior, (C) ventral, (D) anterior.

The type is from the same locality as the type of *G. ocalana*. The diagnosis emphasizes the thick, heavy nature of the xiphiplastron. It is provided with a deep notch posteriorly. The terminal processes are acute, and the anal scute is very short at the midline.

This species is distinct and valid, and can now be completely diagnosed. A number of complete shells, some with limbs and even limb armor, are available from several localities in Florida. It obviously belongs to the *Osborniana*-*Orthopygia*-*Turgida* line, and represents the previously missing Pleistocene representative postulated by Williams in 1953.

GENUS FLORIDEMYS

Floridemys nanus

Figure 25

Bystra nana Hay, 1916.

Floridemys nanus (Hay) Williams, 1950. Williams, 1952; Loveridge and Williams, 1957.

TYPE. USNM 10247, a complete shell of an adult specimen of a distinctive dwarf species of Pliocene testudinine, crushed on the left side of the carapace, and pushed dorsally so that in side view it looks

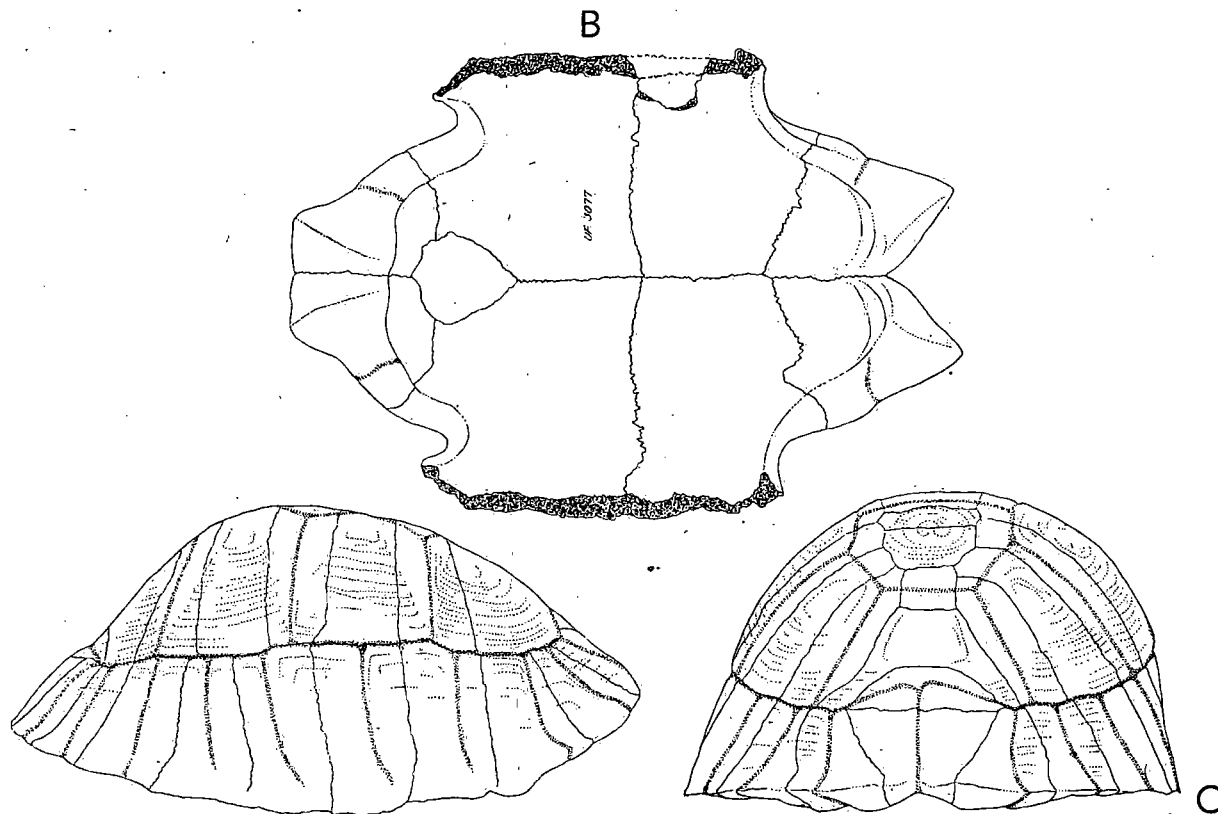


FIGURE 24. Selected views of an adult specimen of *G. incisa* (UF 3077) from Haile VIII A. The posterior view of the carapace (C) illustrates an abnormality in the scutellation (a pair of supracaudal scutes) which is apparently fairly common in this species.

considerably higher than it probably was in life. Originally the type was in the collection of Dr. Henry G. Bystra of Brooksville, Florida.

TYPE LOCALITY AND HORIZON. Collected from a hard-rock phosphate mine, near Holder, Citrus County, Florida; Pliocene (or possibly Miocene), Alachua formation.

DIAGNOSIS. A small species of tortoise distinguished from all other described forms by a transverse gulohumeral sulcus. Other important characters are the truncated epiplastral beak and the straight humero-abdominal sulcus that is directed posteriorly from its median origin.

DESCRIPTION. The type of *Floridemys nanus* has been illustrated by Hay (1916), though the figure leaves something to be desired for tracing articulations and sulcal patterns. An examination of the specimen under different types of light, and both wet and dry, disclosed a number of characters not determinable from Hay's illustration, and not mentioned in the description. The specimen is therefore redescribed.

A dwarf species of testudinine turtle known from a single shell of an adult female turtle 105 mm carapace length. The sulcal growth patterns are moderately developed. The pleurals are alternately wide and narrow at their distal ends. The first pleural is in contact with only the first neural, which is subrectangular in shape. The second neural is hexagonal with the short lateral sides directed posteriorly; the third

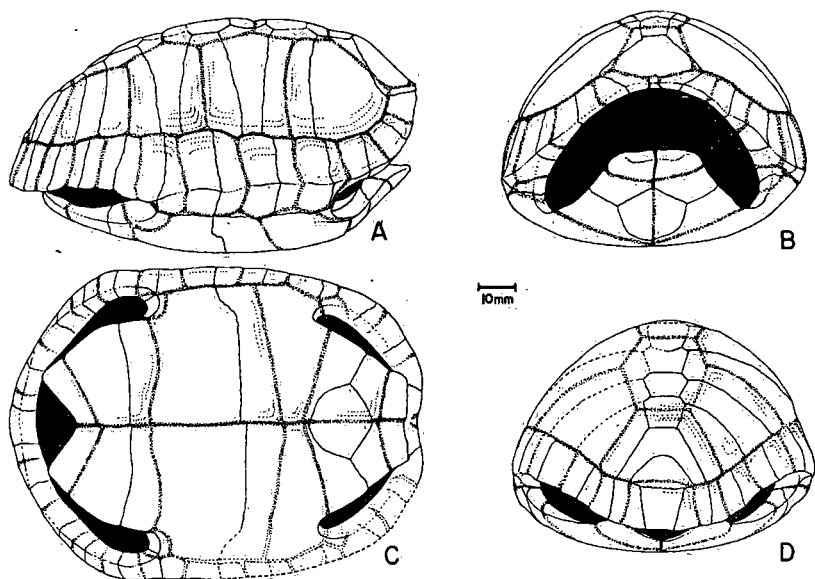


FIGURE 25. Type shell of *Floridemys nanus* (USNM 10247) slightly reconstructed (the original is crushed laterally). (A) lateral, (B) anterior, (C) ventral, (D) posterior.

is apparently quadrangular; the fourth presumably octagonal; and the remaining ones hexagonal with the short sides directed anteriorly. The first suprapygal is bifurcate, the second subtriangular. The pygal is wider dorsally than ventrally. The epiplastral lip is truncated, and does not project beyond the carapace. The gular sulcus does not reach the entoplastron and is almost perpendicular to the main axis of the plastron. The epiplastral bones are short and wide, compared to most species of tortoises. The entoplastron is slightly longer than wide. The gular scute is much shorter than the humeral, but slightly longer than the pectoral. The humeral is also longer than the femoral, and the anal is about as long as the pectoral. The xiphiplastral notch is wide and deep, almost as deep as the length of the xiphiplastral bone along the midline. The hyoplastron is much shorter along the midline than the hypoplastron.

Table 3 gives the pertinent measurements of the type specimen. Some measurements differ slightly from those given by Hay (1916), owing to differences in the way measurements were taken, or to better subsequent preparation of the specimen.

TABLE 3. Shell measurements of the type of *Floridemys nanus*

Carapace length	105 mm	Lip, greatest thickness	11
Carapace width (estimated) ..	80	Lip, greatest length	16
Carapace height (estimated) ..	53	Xiphiplastral external height ..	
Plastron length (midline) ..	96	at hypoplastral articulation ..	11
Xiphiplastral notch depth	12	Xiphiplastral greatest width ..	24
Xiphiplastral notch width	26	Gular length	8
Xiphiplastral length	15	Humeral length	20
Hypoplastral length	32	Pectoral length	6
Hyoplastral length	21	Abdominal length	39
Entoplastral length	18	Femoral length	15
Entoplastral width	17	Anal length	8
Epipastral length	16	Pleural 1 distal length	15
Epipastral width	17	Pleural 1 proximal length	12
Anterior lobe base width	44	Pleural 2 distal length	15
Posterior lobe base width	55	Pleural 2 proximal length	6
Lip, width across anterior ..		Bridge length	54
end	23		

Floridemys nanus is based on a small shell manifesting a single aberrant character. No additional material of this interesting dwarf turtle is available. Williams (1950) is tempted to regard this specimen as an individual variant and, in the absence of other skeletal remains, is apparently not even sure of its testudinine affinities.

Despite the temptation to regard this specimen as an individual variant, the name must be provisionally retained. The aberrant character, the transverse gular-humeral sulcus, is in the form exhibited here, rare in tortoises. . . . When so rare a character is coupled with extremely small size . . . it becomes necessary to withhold judgment until additional material is found.

Although several features of the type suggest emyidine characters, a re-examination of the specimen and the reconstructed shell (fig. 25) leads me to consider it to be a valid testudinine species, though actual proof of such a relationship is certainly lacking. Its relationships might eventually be found to be close to *Stylemys*.

DISCUSSION

Geochelone incisa (Hay) of the southern United States is certainly closely related to *G. osborniana* (Hay) and *G. orthopygia* (Cope) and is here considered to be part of the subgenus *Hesperotestudo*. The subgenus is best characterized by the presence of a caudal buckler. This structure makes its first appearance in *G. amphithorax* (Cope) of the Lower Oligocene of Colorado (fig. 26). Two phyletic lines can be recognized in the subgenus.

THE OSBORNIANA LINE: *G. brontops* (Marsh) of the South Dakota Chadronian seems closely related to *G. amphithorax* and is probably a member of the subgenus *Hesperotestudo*.

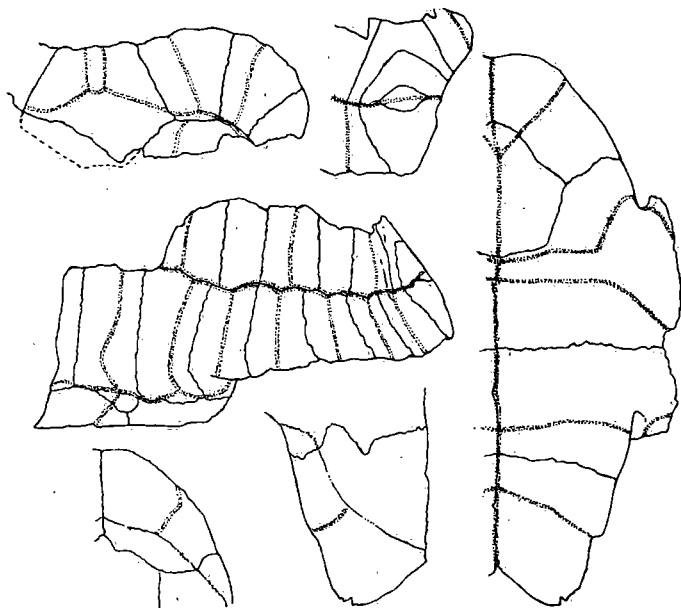


FIGURE 26. *Geochelone amphithorax* (after Hay, 1908).

In these earliest known members of the Osborniana line the shell is relatively thick. The xiphiplastral notch and epiplastral beak are not well developed, being similar to these structures in the subgenus *Caudochelys*. The supracaudal buckler is small and is composed of relatively few, simple ossicles.

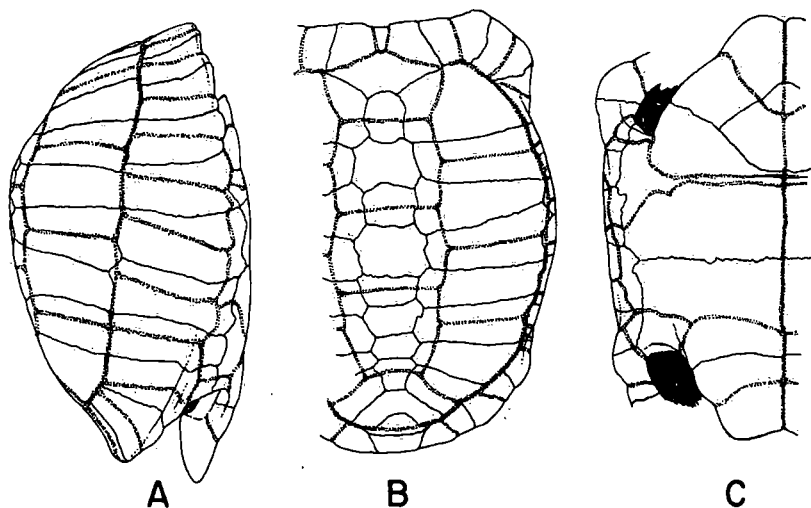


FIGURE 27. Type of *G. osborniana* (AMNH 5868).

Known Miocene members of the Osborniana line are *G. osborniana* (fig. 27) and *G. impensa* (Hay). In both the shell is larger and proportionally thinner than in the Oligocene species. The supracaudal buckler, and the xiphi- and epi-plastra are similar to those of related

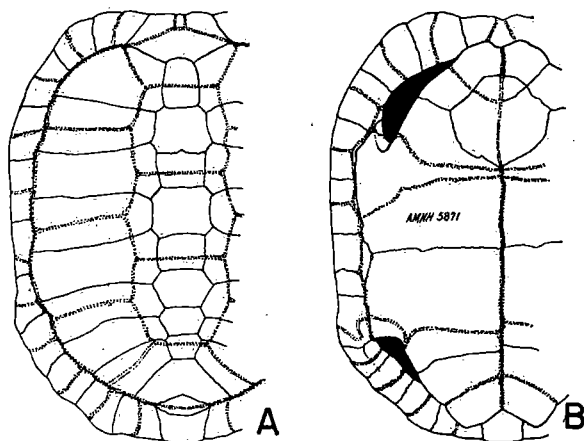


FIGURE 28. Young specimen of *G. osborniana* (AMNH 5871).

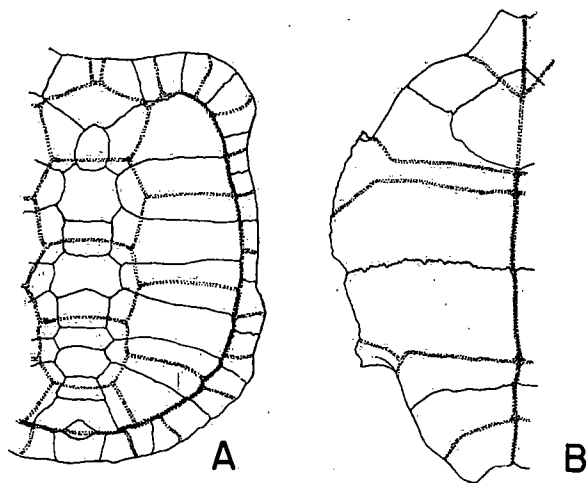


FIGURE 29. Adult specimen of *G. orthopygia* (after Hay, 1908).

forms from the preceding epoch. *G. angusticeps* (Matthew) is a smaller but more rugose Miocene species that appears to be close to the Pliocene *G. orthopygia*.

The last member of the Osborniana line is *G. orthopygia* (figs. 28, 29) of the Lower Pliocene. This is a large, thin-shelled species with a large but simple supracaudal buckler. It represents the culmination of a phyletic line, which, since the Oligocene, tended toward moderate gigantism, a smooth thin shell, and a simple supracaudal buckler.

THE TURGIDA LINE: *Geochelone turgida* (Cope, 1892) of the Pliocene of the Great Plains represents the extreme specialization of this phyletic line. It is small and highly rugose. The supracaudal buckler is proportionally large, but not so rugose as that in some Pleistocene forms. *G. kalganensis* (Gilmore, 1931) from the Kalgan area, northern China, is obviously closely related to *G. turgida* on the basis of shell rugosity, size, and sulcal patterns. It represents the only record of the subgenus *Hesperotestudo* outside continental North America. Unfortunately no stratigraphic data are available with the specimen; it is assumed to be Tertiary in age. *Testudo insolitus* Matthew and Granger (1923) of the Lower Oligocene of Mongolia also may belong to this line, though the evidence is inconclusive.

In the southeastern United States the only known Pleistocene member of this phyletic line is *G. incisa*. The line is represented in the Pleistocene of the Great Plains area, but complete shells are not available. Although definite allocations are impossible at present, *G. equi-*

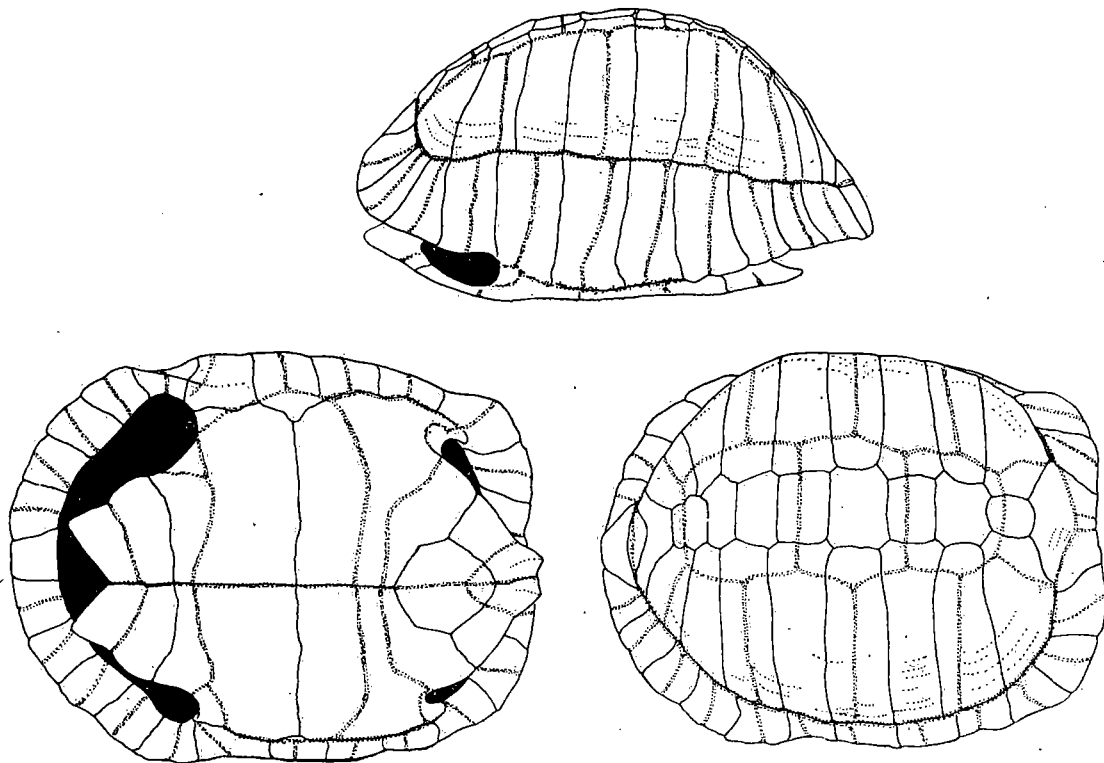


FIGURE 30. Type of *G. wilsoni* (Tex. Mem. Mus. 933-3585), a Texas Pleistocene species closely related to *G. incisa*.

comes (Hay, 1917) probably belongs to this line and, in all likelihood is the western Pleistocene representative of the subgroup. The type (USNM 10944) is an epiplastron. The general shape of the element, particularly its thickness, is almost identical to that of *G. incisa*, from which I infer a close relationship. *G. wilsoni* (Milstead, 1956) of the Pleistocene of Texas (fig. 30) is close to *G. incisa*. *G. johnstoni* (Auffenberg, 1962), from City Canyon, near Canyon, Texas, is similar to *G. incisa*, and closely related to it. It is intermediate between *G. turgida* and *G. incisa*, both structurally and temporally. *G. riggsi* (Hibbard) is also intermediate (fig. 31), but much closer to *G. turgida*.

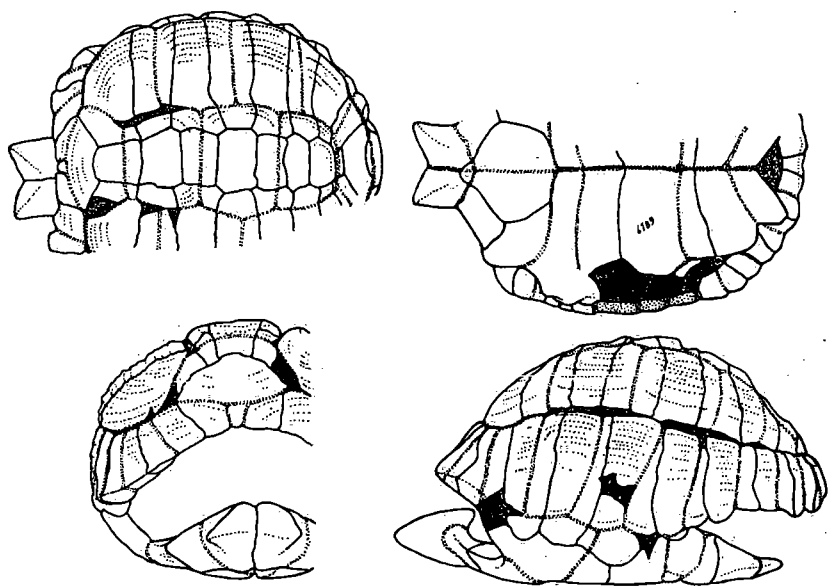


FIGURE 31. Paratype of *G. riggsi*, a species seemingly intermediate between *G. turgida* and *G. incisa*.

The Turgida-Riggsi-Johnstoni-Incisa sequence is one in which several trends seem fairly clear (fig. 32). These trends in structural changes with time from Pliocene to Pleistocene include: 1) increase in size, 2) decrease in proportional shell thickness, 3) decrease in rugosity of shell, and 4) additional complexity of the supracaudal buckler through fusion of a larger number of ossicles and a greater degree of ornamentation on the surface of each fused member.

Possibly this line was present in the eastern United States during the Pliocene, though it has not yet been found there. If it was present,

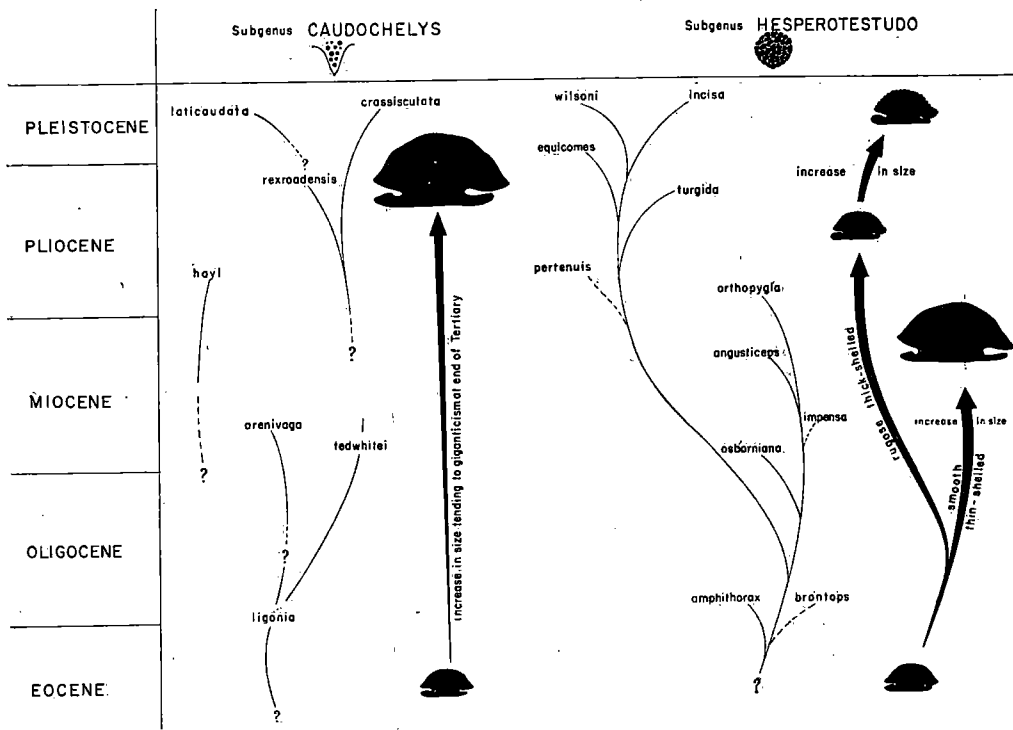


FIGURE 32. Some major evolutionary trends, and the presumed phyletic relationships within the better known species of the subgenera *Caudochelys* and *Hesperotestudo*.

a second species of Pliocene *Geochelone* from Florida is masquerading as *G. hayi*.

The subgenus *Caudochelys* probably begins somewhere near *G. uintensis* (Gilmore) of the Upper Eocene of Utah. *G. ligonia* (Cope, 1873) of the Lower Oligocene of Colorado is probably a member of this subgenus. *G. arenivaga* (Hay, 1907) of the Nebraska Miocene Harrison formation may belong here as a Plains representative, and *G. tedwhitei* (Williams, 1953), Lower Miocene of Florida, is probably its eastern counterpart. *G. hayi* (Sellards, 1916), Pliocene of Florida, and *G. rexroadensis* (Oelrich, 1953), Pliocene of Kansas, may be east-west representatives, though the former is probably more distantly removed from the main line. The latter is certainly closely related to several Pleistocene forms such as *G. crassiscutata* of Florida. Western Pleistocene counterparts may include *G. laticaudata* (Cope, 1889).

Relationships within the subgenus *Caudochelys* seem more obscure than those in *Hesperotestudo*, perhaps because of the basic similarity of its several known forms. No major trends other than increase in size are recognized.

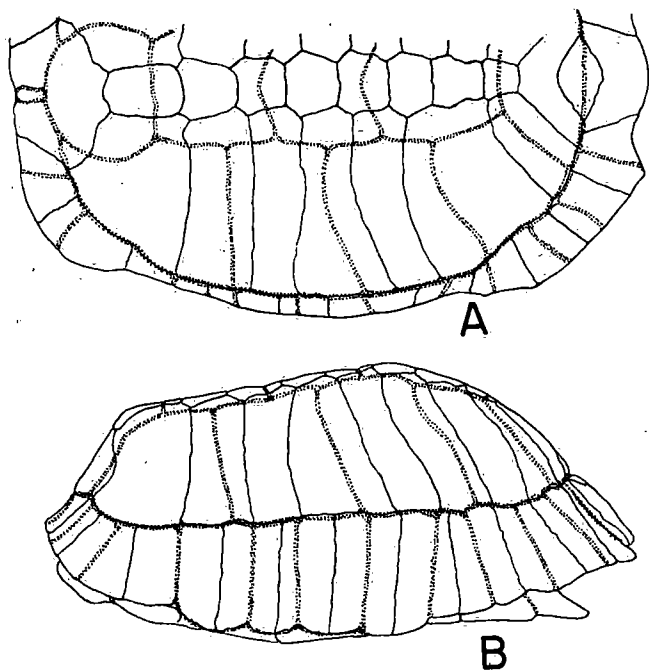


FIGURE 33. Type of *G. primaeva* (UMMP 25758).

In addition to the species discussed above, several other tortoises are known only from remains so fragmentary, or of a type so inadequate for comparison that their relationships remain obscure. Such little-known Pleistocene species are: *G. annae* (Hay, 1923), and *G. francisi* (Hay, 1923). *Testudo munda* Hay (1920) is based on portions of the carapace and plastron of a small turtle (USNM 8944) collected by Ira Sayles in 1885 in a Pleistocene deposit near Whitesburg, Hamblen County, Tennessee. The type is not a testudinine at all, but an emydine. The specimen is, in fact, part of an individual of *Terrapene carolina*, and the name *T. munda* should be added to the synonymy of that species. *G. gilberti* (Hay, 1902) is an obscure Pliocene form. The little-known Miocene forms are: *G. farri* (Hay, 1908), *G. ducatelli* (Collins and Lynn, 1936), *G. undata* (Cope, 1884), and *G. klettiana* (Cope, 1874). Oligocene forms are: *G. quadrata* (Cope, 1884), *G. peragrans* (Hay, 1906), *G. cultrata* (Cope, 1873), *G. exornata* (Lambe, 1913) and *G. thompsoni* (Hay, 1908). A testudinine turtle described as *Testudo primaeva* Oelrich (1950), from the Madison River area, Montana, is apparently a primitive form (fig. 33) probably distantly related to *Caudochelys* and *Hesperotestudo*. The shell is similar to that of *Gopherus emilae* (Hay, 1907) from the Rosebud of South Dakota, including the presence of a complete set of hexagonal neurals. *Gopherus copei* (Koerner, 1940) from the Deep River Miocene of Montana is also similar, though it differs in several minor respects.

Geochelone hayi (Sellards, 1916) may belong to the genus *Gopherus*, as Williams (1952) suggests. Better preserved specimens should settle this point easily.

Several problems are suggested by the separation of *Hesperotestudo* of Williams into two subgenera. Both lines apparently arose from *Hadrianus*, or a *Hadrianus*-like ancestor. Thus, further study may show the subgenus *Hadrianus* to be composed of several subgroups. One of these may be ancestral to *Geochelone*. Perhaps lines ancestral to *Hesperotestudo* and to *Caudochelys* may be recognized. Another group may be ancestral to *Gopherus*, still another to *Stylemys*.

The last genus presents particularly interesting problems, e.g. 1) the apparent relationship between this genus and *Gopherus*, and 2) a comparison of the Old and New World forms. Unfortunately, no nonshell elements are known in *Floridemyx nanus*. The proportions of the shell are markedly similar to those of *Stylemys*, particularly *S. conspecta* Hay (1908) from the John Day beds of Oregon. In *Floridemyx* the third neural is quadrangular, as it is in many specimens of *Stylemys*, most *Geochelone*, and no known *Gopherus*. Unfortunately

the single specimen of *Floridemys* is fractured, and it is impossible to ascertain the shape of the second neural. In *Stylemys conspecta* it is octagonal. The only major difference between them is the peculiar transverse position of the gulohumeral sulcus in *Floridemys*. *S. conspecta* is the most *Testudo*-like in the arrangement and proportions of the bony elements of the shell. The most recent, and thus most interesting species of *Stylemys* in this regard is *S. calaverensis* Sinclair from the Miocene of California. Unfortunately the fragmentary type is the only specimen. It differs from other species in possessing a first neural that is as broad as the anterior edge of the second, a character also found in *Floridemys nanus*.

Supracaudal dermal armor, to my knowledge, has not been found with any North American Eocene testudinine. Thus, little can be said regarding the ancestry of the remarkable caudal buckler in *Hesperotestudo*. Of possible significance is the genus *Cymotholcus*. Two North American species are recognized: *Cymotholcus longus* Clark (1932) and *C. schucherti* (Hay, 1902). The latter is not well known, but the former is represented by a shell and parts of the skeleton. Its relationship to other Eocene testudinines remains obscure, though Clark suggests a possible relationship to *Stylemys*. Of particular interest in a consideration of the ancestry of *Hesperotestudo* is the tail of *C. longus*. According to Clark,

... Maximum downward projection of the tail would not suffice to allow the tip to touch the plastron. Moreover, because the anal portion of the posterior lobe of the plastron is contained within the floor of the carapace, rather than being ventral to it, the skin of the dorsal region must have stretched horizontally so that the external tail was at most a tiny projection, and very possibly was not present at all.

Though the tail of *C. longus* is very short, the transverse processes of the vertebrae are not developed to support a buckler. A single dermal ossicle of the caudal area, which was associated with the specimen, could not have been part of such a fused unit. However, in looking for a presumed ancestral form for *Hesperotestudo*, a short, or even nonexistent external tail is important. Thus, *Cymotholcus* may be an ancestor to the *Hesperotestudo* line, although this possibility is suggested now only as an undocumented idea.

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